BRAUERIA (Lunz am See, Austria) 31: 9-10

Larval and pupal case building in Trichoptera: A comment to articles of G. B. Wiggins and H. Malicky in Braueria 27 and 28

H.W. BOHLE

Referring to the cited articles of Hans Malicky and Glenn Wiggins there are two questions:

1. How far do accomplished trichopteran buildings (cases etc.) represent building behaviours.
2. What are the phylogenetic relationships between larval and pupal cases, especially in the Integripalpia ?

The great variety of design among caddis houses, more or less specific of the taxonomic units, leads to the assumption of different genetically determined programs. This includes the variability of building behaviour during larval ontogenesis as well as the adaptive flexibility, more or less pronounced in the different taxa. The building activity of the larvae includes searching for an appropriate place, selection and adaptation of building material, inserting and fixing it with silk, and especially in the Integrepalpia, the construction of the inner lining, the rear apertur or – in pupal cases – the porous silken opercle of the tube-case and shortening of the tube from time to time. Prior to each larval moulting and to pupation, fixing of cases with silken threads usually happens. In many species, full grown larvae are searching specific places for pupation, e.g. to assemble to aggregations. After all, the construction plan, leading to the specific shape of the case, is part of the genetic program.

From the structure of the building we can refer to some of the building activities, especially the construction plan, the result of the selection of building material, and – by a thorough analysis – also to some of the results of the different spinning activities (BOHLE 1972, 1974). If we are able to compare the products of different ontogenetic phases and different origins it should be possible to describe and perhaps to explain the structural variance. In this way we gain important information on building behaviour. Nevertheless, some aspects, e.g. searching behaviour or the details in the sequence and form of building motion, are not to grasp.

Direct and accurate investigation of a rather complex behaviour, as in case construction, costs much time and makes it difficult to compare a large number of objects. Extensive control is necessary in order to comprehend the variability on the individual scale and between species of a taxonomic group. The comparative analysis of case building behaviour by STUART & CURRIE (2001) contains some deficits, which could be avoidable, regarding e.g. the structure of the silken layers.

If we want to reconstruct the phylogenetic relationship between pupal and larval buildings, we should, as a first step, explain those general phylogenetic relationships which are important for the definition of plesiomorphic and apomorphic traits. Larval cases of Glossosomatidae are in the dome shaped upper part structurally nearly identical with the pupation chamber of Rhyacophilidae (BOHLE & FISCHER 1983, WIGGINS & WICHARD 1989). The tortoise larval case of the Glossosomatidae is completed underneath by a plate with two foramina near the border. A continuous inner silken layer - typical for Integripalpia – is lacking. Within the Glossosomatidae the structural complexity increases from species of the genus *Glossosoma* to *Agapetus, Synagapetus* and *Catagapetus*. It seems that the portable larval case is an adapted pupal case. It is newly built in each larval stage and, as a general rule, also for pupation. The underside plate of this case is removed previous to the fastening to the ground. Although an entirely new case is built, it is constructed as an adjunct to the preceding one or as a provisorial building, perhaps an analogy to *Phryganopsyche*. All traits of higher complexity of the dome (e.g. the silken fringe, the lids of ventral foramina, the two ventilation-pores in the ridge of the dome of *Synagapetus*) are reduced in this stage. Under this dome-shaped "outer cocoon" the silken inner cocoon is spun, entirely separated from the stony walls. This similarity between Rhyacophilidae and Glossosomatidae supports the taxonomic identity of the Spicipalpia (WIGGINS & WICHARD 1989).

Similarities to the Integripalpia concerning the construction of larval and pupal cases are not obvious. Tube - or tunnel-shaped silken larval residences, either fixed to the substrate or portable, are widespread in Lepidoptera, the probable sister group of Trichoptera. According to ROSS (1964) all silken buildings of caddis larvae, including the pupal cocoon, are to derive from this system. The pupal cocoon of these ancestors is constructed of three layers, first the outer layer, which can include extraneous material, second the loose, spongy middle layer and finally the closely woven inner layer. The pupation chamber of Annulipalpia/Curvipalpia seems to represent this type (WEAVER & MORSE 1986, WIGGINS 1992, WIGGINS & WICHARD 1989). The portable tube-case of Integripalpia, according to this postulation, consists of the outer and inner layer of the cocoon-wall, the middle layer is lost: The larval case – at least in respect to the inner layer – should be "a premature building of the pupal case" (ZWICK 1998). A construction of a separate (inner) cocoon for pupation, as it is usual in Glossosomatidae, does not take place. It could also be possible to derive the portable tube case from the silken tubes of larval ancestors (e.g. proposed by MILNE & MILNE 1939 with functional arguments), particularly because silken tubes or tunnels are found in different functions, as retreat in net-building taxonomic groups, as ramified tunnel–residence in Psychomyidae, or as temporary precoursor-construction as it is found sometimes in Glossosomatidae (BOHLE & FISCHER 1983, HANSELL 1968). The existence of the inner silken layer as homologue to the inner cocoon layer in larval tube cases and the lack of a separated pupal cocoon-lining in Integripalpia are traits which confirm the derivation from pupal stages of ancestors.

The discussion in Braueria 27 and 28 concerns pupal cases of some Linnephilidae and of *Yphria californica* (Phryganeidae) and *Phryganopsyche latipennis* (Phryganopsychidae). The pupal cases of the presented Limnephilidae, of *Yphria* and of *Micrasema longulum* (ZWICK 1998) show the typical tube structure but differ from the appertaining larval case in some characteristic attributes: The cases are straight, not curved, parallel sided which means not tapering to the hind end, independent of the form of the larval case. Additionally, these cases are often distinguished by a different selection of building material. As a rule we assume that these pupal cases are constructed as an adjunct to the larval case and then cut free. Finally, the anterior and the posterior foramen of the case are closed by apertures, porous silken plates or other forms of coverings.

Change of constructive design is found also in the course of larval ontogeny in many taxonomic groups, often coupled to the change in selection of building material or the transition to a secret-case (e.g. HANNA 1961, HANSELL 1972, 1984, BOHLE 1974, SATTLER 1957, ZINTL 1974). The uniform, not tapering pupal tube–case could result from an adaptive behaviour because in the full grown larva the size of the body remains nearly constant (HANNA 1960). The structure of the coverings of the terminal openings of the pupal case tube is manifold, especially in Linnephilidae. Dome-shaped coverings similar to those of *Yphria* (WIGGINS 2001) can be found e.g. in *Cryptothrix nebulicola* (Drusinae) (BOHLE 1987). A corresponding structure to the "stout meshwork of silk" "beneath the bulbous enclosure" of *Yphria* seems to be absent or could be integrated in the outer enclosure. A short description of the pupal case of *Phryganea grandis* (THIENEMANN 1905) perhaps means a similar inner structure (-"sind die Verschluß-" Membranen"... ganz weitmaschige Netze"...), with "eine große Menge quer gelegter Pflanzenfasern..., so daß eine dichte, allen Schmutz abhaltende Reuse entsteht" as (homologous?) outer covering. On the other hand, the construction of a completely new pupal case probably indicates a plesiomorphic trait if we accept that the basal ancestors already had tube-formed cocoons with an outer and inner layer. A homology with the shape of the outer layer of the pupation chamber of the Spicipalpia and Annulipalpia is not discernible. It should not be surprising if there exists some variability in the utilisation of sections of larval case as pupal house because the shape is very similar and the functionality is given if the width is suitable. Nevertheless, the construction of separate pupal cases is not limited to one monophyletic group of Integripalpia (MALICKY 2000), and it occurs side by side in the same taxonomic group with species using larval cases for pupation as in Limnephilidae and Brachycentridae. That's why it remains uncertain if this is an atavistic trait or convergent development (ZWICK 1998).

It is difficult to evaluate the homology of the considered traits of the examples regarded so far, because most of them are rather unspecific, which raises the probability of convergency. Only the lamination of the wall of the cases may be an exception. Unfortunately we have only sporadic information on this topic. The

general rule seems to be the composition of two layers (BOHLE 1972, 1974). WILLIAMS & PENAK (1980) describe three layers for *Phyrganea cinerea* from microscopical cross-sections of the larval case (the middle-layer "appeared to be continuous circular threads – laid down on the inside surface of the case. On top of this was placed a layer of diagonally criss-crossing fibers...." = the inner layer). Referring to ROSS (1964) this would be the most plesiomorphic larval case known so far. This structural peculiarity seems to be an important trait and we should try to find its traces elsewhere, especially in Phryaneidae, which are characterized also by other plesiomorphic traits (cf. phylogenetic tree from WEAVER 1984).

Phryganopsyche latipennis, as described by WIGGINS, obviously represents the most primitive or plesiomorphic example. The pupal case with its ovoid shape and the "loose weave of the inner silken cocoon" is integrating an independent closed building with a three-layer-cocoon, perforated only by some ventilation pores (as far as I understood the description) (WIGGINS & WICHARD 1989, WIGGINS 2001). It would be of special interest to find out more about the structure of the flexible wall of the larval case, if there are differences concerning the two-layer construction. The shape of the pupal case and the structure of its wall of *Phryganopsyche* resemble pupal buildings of Annulipalpia (e.g. of some Philopotamidae: WIGGINS & WICHARD 1989), with the difference that the outer layer is not closed ventrally. In all the other examples of the Integripalpia the pupal cases retain the tube shape.

References

BOHLE, H.W. (1972). Vergleichende Untersuchungen über den frühlarvalen Köcherbau der Brachycentridenarten *Micrasema minimum* MACLACHLAN und *Brachycentrus montanus* KLAPALEK (Trichoptera, Insecta). Zool. Jb. Syst. 99: 507-544.

BOHLE, H.W. (1974). Der frühlarvale Köcherbau von *Micrasema longulum* MCL. (Trichoptera, Brachycentridae). Int. Revue ges. Hydrobiol. 59: 403-420.

BOHLE, H.W. & FISCHER, M. (1983). Struktur und Entstehung der Larven- und Puppengehäuse einiger Glossosomatidae und Rhyacophilidae, insbesondere bei *Synagapetus iridipennis* (Trichoptera; Rhyacophiloidea). Entomol. Gener. 9: 17-34.

BOHLE, H.W. (1987). Drift-fangende Köcherfliegen-Larven unter den Drusinae (Trichoptera: Limnephilidae). Entomol. Gener. 12: 119-132.

HANNA, H.M. (1960). Methods of case-building and repair by larvae of caddis flies. Proc. R. Ent. Soc. Lond. A 35: 97-106.

HANNA, H.M. (1961). Selection of materials for case-building by larvae of caddis flies (Trichoptera). Proc. R. Ent. Soc. Lond. A 36: 37-47.

HANSELL, M.H. (1971). Case building behaviour of the caddis fly larva, *Lepidostoma hirtum*. Journal of Zoology, 167: 179-192.

HANSELL, M.H. (1984). Animal architecture & building behaviour. London: Longman.

MALICKY, H. (2000). Which caddis larvae construct a new case ?. Braueria 27: 19-20.

MILNE, M.H. & MILNE, L.J. (1939). Evolutionary trends in caddis worm case construction. Ann. Entomol. Soc. of America. XXXII: 533-541.

ROSS, H.H. (1964). Evolution of caddisworm cases and nets. American Zoologist, 4: 209-220.

SATTLER, W. (1957). Beobachtungen an den Larven von *Crunoecia irrorata* CURT. (Trichoptera). Berichte der Limnologischen Flußstation Freudenthal Außenstelle der Hydrobiologischen Anstalt der Max-Planck-Gesellschaft III. 18-32.

STUART, A.E. & CURRIE, D.C. (2001). Using caddisfly (Trichoptera) case-building behaviour in higher level phylogeny reconstruction. Can. J. Zool., 79: 1842-1854.

THIENEMANN, A. (1905). Biologie der Trichopteren-Puppe. Zool Jahrb. Syst. XXII, 489-517.

WIGGINS, G.B. (1992). Comments on the phylogeny of pupation behavior in Trichoptera: A response to Weaver. Cladistics 8: 181-185.

WEAVER, J.S. & MORSE, J.C. (1986). Evolution of feeding and case-making behavior in Trichoptera. J. N. Am. Benthol. Soc. 5: 150-158.

WIGGINS, G.B. (2001). Construction behavior for new pupal cases by casemaking caddis larvae: Further comment. (Trichoptera: Integripalpia). Braueria 28: 7-9.

WIGGINS, G.B. & WICHARD, W. (1989). Phylogeny of pupation in Trichoptera, with proposals on the origin and higher classification of the order. J. N. Am. Benthol. Soc. 8: 260-276.

WILLIAMS, D.D. & PENAK B.L. (1980). Some aspects of case building in *Phyryganea cinerea* Walker (Trichoptera: Phryganeidae). Anim. Behav. 28: 103-110.

ZINTL, H. (1974). House building: problems about the spontaneous change of the architectural style in the larva of *Potamophylax latipennis* (Curt.) (Trichoptera, Limnephilidae). Proc. of the First Int. Symp. on Trichoptera. 187-201.

ZWICK, P. (1998). *Micrasema longulum* (Trichoptera: Brachycentridae) builds a special pupation chamber. Annls. Limnol. 34: 437-444.

Dr. Hans Wilhelm BOHLE
Grüner Weg 18
D - 35041 MARBURG

Potamophylax rotundipennis